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Coherence and phase locking of intracerebral activation during visuo- and audio-motor learning of continuous tracking movements

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Abstract The aim of the present study was to assess changes in EEG coherence and phase locking between fronto-parietal areas, including the frontal and parietal motor areas, during early audio- and visuo-motor learning of continuous tracking movements. Subjects learned to turn a steering-wheel according to a given trajectory in order to minimise the discrepancy between a changing foreground stimulus (controllable by the subjects) and a constant background stimulus (uncontrollable) for both the auditory and the visual modality. In the auditory condition, we uncovered a learning-related increase in inter-hemispheric phase locking between inferior parietal regions, suggesting that coupling between areas involved in audiomotor integration is augmented during early learning stages. Intra-hemispheric phase locking between motor and superior parietal areas increased in the left hemisphere as learning progressed, indicative of integrative processes of spatial information and movement execution. Further tests show a significant correlation of intra-hemispheric phase locking between the motor and the parietal area bilaterally and movement performance in the visual condition. These results suggest that the motor-parietal network is operative in the auditory and in the visual condition. This study confirms that a complex fronto-parietal network subserves learning of a new movement that requires sensorimotor transformation and demonstrates the importance of inter-regional coupling as a neural correlate for successful acquisition and implementation of externally guided behaviour.

Keywords EEG · Coherence · Phase locking · Motor learning · Sensorimotor · Alpha rhythm

Introduction

Movement in everyday life is often guided by external stimuli. For this, the association of external cues with motor commands is essential. Learning to perform new movements that are guided by external stimuli places high demands on the neuronal system, because different brain areas have to be mobilised to cooperate in a network-like fashion so that the cue-movement association can be established. A practical method with which to register neurophysiological cooperation is to measure and compute coherence and phase locking of oscillatory neuronal activity on the basis of surface EEG signals. For example, Classen et al. (1998) uncovered a significant increase in intra-hemispheric coherence between electrodes placed over central and occipital regions during visuomotor tracking compared with visual or motor control conditions. Several more recent studies have used EEG-based coherence and phase-locking measures to study changes in intra- and inter-hemispheric cooperation during the acquisition or optimisation of uni- and bimanual motor tasks (Andres et al. 1999; Serrien and Brown 2003; Gerloff and Andres 2002). Andres et al. (1999) and Gerloff and Andres (2002) show enhanced inter-hemispheric coherence between relevant brain areas during early learning of bimanual movements and decreased coherence in later learning stages. This result reflects increasing independence in the operation of both hemispheres (and in particular of motor areas) with increasing bimanual skill. Similarly, Serrien and Brown (2003) demonstrated that with increasing practice the coherence between the sensorimotor areas

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decreases in the alpha- and beta-band but increases between the prefrontal areas for the gamma-band. These data were taken as evidence for the suggestion that the strength of cortico-cortical connectivity is adaptively modified across regions during early sensorimotor learning.

To the best of our knowledge, most EEG or MEG studies examining interregional coherence in the context of movement learning were based on discrete uni- or bimanual movements (e.g. finger tapping, button presses) (Andres et al. 1999; Andres and Gerloff 1999; Gerloff and Andres 2002) or on coordination of continuous bimanual movements which do not require continuous adaptation to external cues (Serrien and Brown 2002; Serrien and Brown 2003). In contrast to these studies the present study focuses on cortical dynamics associated with the acquisition of new visuo-motor and audio-motor continuous bimanual tracking movements. In short, the subjects learned to bimanually manipulate a steering-wheel according to a given trajectory in order to minimise the discrepancy between a changing foreground stimulus (controllable by the subject using the steering wheel) and a constant background stimulus (uncontrollable and provided by the computer program). In the visual tracking task the foreground stimulus consisted of a continuously changing visual signal while in the auditory task the foreground stimulus consisted of a continuously changing auditory signal.

When guided by continuously available external visual and auditory information, as during continuous tracking movements, motor control requires ongoing processing and transformation of sensory information into motor commands. Thus, there is ongoing distributed computation in a sensorimotor network including the sensory, the parietal, the premotor and the primary motor areas. Because there is currently no study available reporting coherence and phase locking data during the acquisition and optimisation of continuous tracking movements we have designed the present study. Previous movement learning studies (using bimanual tapping movements without relying on strong sensory input as during continuous tracking movements) showed decreased inter-hemispheric coupling especially in later learning phases, supporting the idea of increasing inter-hemispheric independence with increasing bimanual movement proficiency. However, is there also a decrease of interhemispheric coupling during the course of continuous bimanual tracking movement learning during which the processing of sensory information and not bimanual coordination is essential? In addition, it is not known whether there are changes in intra-hemispheric coherence and phase locking during the course of this kind of motor task. In the light of the well-known binding theory (Singer 1993; Singer and Gray 1995) one might anticipate increased coherence between the participating brain regions with increasing practice. Furthermore, it has to be determined

whether there is a difference in continuous visual versus continuous auditory tracking in terms of coherence and phase locking. In summary, many questions are unanswered so far in the context of cortical dynamics during learning of visuo- and audio-motor tracking movements. Based on the results of the studies mentioned above, we assume that coherence and phase locking between frontal and parietal brain regions will increase during the course of learning progress. We hypothesise that if coherence is functionally relevant, the coherence measures for the fronto-parietal network will be significantly related to increasing movement proficiency.

Finally, it is necessary to mention that we used an alternative and recently developed method of coherence and phase locking computation, which is based on estimated intracerebral activation sources (Lehmann et al. 2006). This approach may provide more direct information about interaction between the generators of EEG-activity.

Methods and materials

Subjects

Nineteen (9 women and 10 men) healthy right-handed volunteers took part in the experiment. Their mean age was 33.6 ± 12.1 (SD) years. Health was measured using appropriate questionnaires. Handedness was assessed with the Annett-Handedness-Questionnaire (Annett 1970; Annett 1992). The local ethics committee approved the study and all subjects gave written informed consent.

Experimental design

The basic principle of our movement task is to increase tracking precision during the course of learning. In a compensatory motor tracking paradigm, subjects learned to turn a steering-wheel according to a given trajectory in order to minimise the discrepancy between a changing foreground stimulus (controllable by the subject) and a constant background stimulus (uncontrollable). We attached the steering-wheel to a potentiometer in order to measure steering movements between -125° and $+125^\circ$, with 9 bit precision (512 steps).

Since classical tracking tasks mostly involve horizontal eye-movements, which contaminate EEG-recordings of premotor areas, we designed two tracking tasks (an auditory and a visual) with which to prevent at least gross horizontal eye-movements. In the *visual task* condition, subjects were seated in front of a 17" monitor (resolution of 800×600 pixels), with an eye-monitor distance of about 0.65 m and an angle of vision of 33.6° to the left and the right side. The foreground stimulus consisted of a square

framed by a lime-coloured border with a dimension of 50 pixels presented in the centre of the visual field. Without the subject's intervention, the field of the square within the lime-coloured margin (foreground stimulus) changed its tone on a greyscale in a predefined manner not obvious to the subjects. This changing target was controlled by commercial experimental software (Presentation, Version 0.81, Neurobehavioral system, Albany, CA, USA). The background of the screen itself presented in grey was used as the background stimulus. At the beginning of the trial, the foreground stimulus (square) was presented in the same grey tone as the background stimulus and was only distinguishable by its coloured frame. The grey tone changed from dark (0 cd/cm^2) to bright (250 cd/cm^2). The stimulus was built up by 1,000 data points. The tone of the foreground stimulus was refreshed 1,000 times in 16.66 s trial time (refresh rate of monitor 60 Hz).

While the centre of the square changed in brightness according to the predetermined pattern the subjects were required to prevent this change by manipulating the steering-wheel (SideWinder Force Feedback Wheel, Microsoft). Thus, the subjects' task was to conduct continuous tracking movements and to learn the movement required to keep the grey tone of the foreground stimulus as close as possible to that of the background stimulus.

In the *auditory task* condition, the changing foreground stimulus was a train of short (8 ms) sine tones, which changed their frequency in the range of 400–4,500 Hz in a predefined manner. The background stimulus was a constant sine tone of 2,875 Hz. The stimuli were presented via commercial headphones (Technics Stereo Headphones RP-F550). The refresh rate of the tone was also set at 60 Hz. The duration of the tone was 8, 4 ms fade-in and 4 ms fade-out. The intensity of the tone was adjusted to individual preference. The lime-colour framed square appeared as a fixation point without changing colour. As in the visual task, the subjects had to learn to turn the steering-wheel so as to keep the tone of the foreground stimulus and that of the background stimulus as similar as possible.

Brightness of the square and frequency of the foreground tones were parameterised according to a 256-step grey- or frequency scale. The difference between the foreground stimulus and the background stimulus was continuously calculated by registering the position of the

steering-wheel at each of the 1,000 data points forming the sequence of one movement. The difference between the position of the steering-wheel and the required position given by the target track was taken as a measure of precision of the tracking performance. The subjects were informed about the performance directly after each trial by presenting the deviation from the target track (sum of data point differences between foreground and background stimulus). There were 30 trials for each modality.

The subjects had time to practice before the beginning of data collection in order to become familiar with the principle of the compensatory tracking task and the handling of the steering-wheel. Subjects performed 30 trials of each modality in one session. Two different movement trajectories were used, counterbalanced over the visual and auditory task condition. Half of the subjects started with the visual task the other half started with the auditory task in randomised order. The single trials were initiated by the subjects themselves, pressing a start button on the steering-wheel (Fig. 1).

Data acquisition

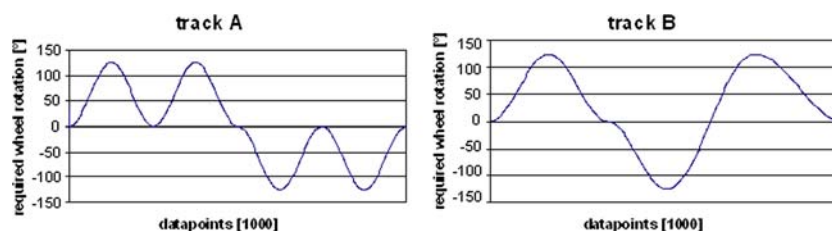
Continuous EEG was recorded from 32 (silver-silver chloride) surface electrodes, mounted with the "Easy cap System" ("Easy Cap System", International 10-20 system, FMS Falk Minow Services, Herrsching-Breitbrunn, Germany) (Fig. 2). The electro-oculogram (EOG) was recorded from two additional electrodes placed below the outer canthi of each eye. A BrainVision amplifier system and Recorder (Quik amp 40 BrainProducts, Germany) were used to record the data (electrode impedances $< 5 \text{ k}\Omega$, 0.5–70 Hz, 500 samples/s).

Data analysis

Behavioural data

We compared the steering-wheel position with the required target position separately for each of the 1,000 data points, which together form the sequence of one movement, and calculated the mean absolute deviation for each movement (Matlab Version 6.5, The MathWorks, Inc., Natick, MA, USA). The first ten of the 30 movements were pooled to

Fig. 1 Movement trajectories two different movement trajectories *track A* and *track B* were used, counterbalanced over the visual and the auditory task



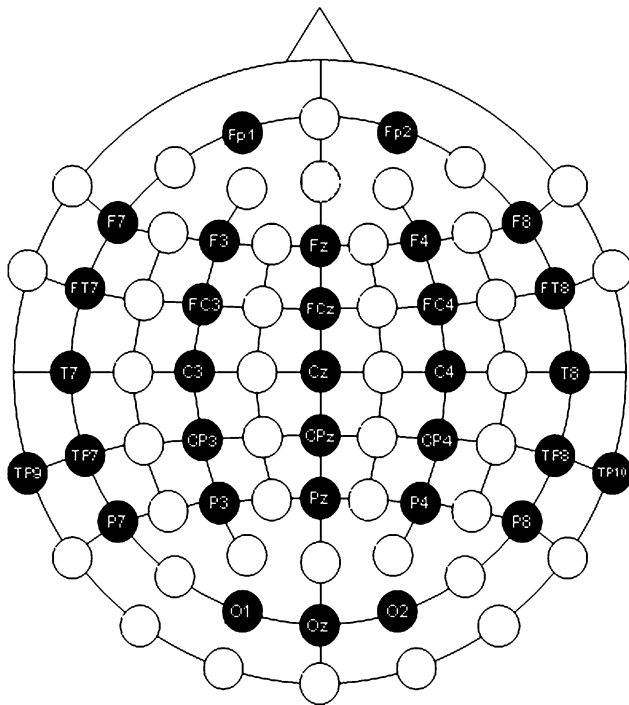


Fig. 2 Electrode montage the EEG was recorded from 32 scalp electrodes in the following positions *Fp1/2, F3/4, F7/8, Fz, FCz, FT7/8, FC3/4, T7/8, C3/4, Cz, TP7/8, TP9/10, CP3/4, CPz, P7/8, P3/4, Pz, O1/2, and Oz*

phase 1 and the last ten movements to phase 3. If the mean absolute deviation in phase 3 was significantly lower than the mean absolute deviation in phase 1, then the subject was labelled as a Learner (two-tailed independent samples *t*-test $P < 0.05$). Behavioural data was subjected to repeated measures ANOVA with the following factors: “condition” (auditory, visual), “phase” (1 = early, 3 = late) and an additional factor between subjects: “Learners” (Learners, Non-Learners).

Electrophysiological data

EEG-raw data were bandpass filtered from 1.5 to 30 Hz. In order to cope with EEG eye artefacts (eye blinks, eye movements) we ran an ICA (independent component analysis) algorithm provided in the BrainVision software to avoid the considerable loss of collected information that occurs when rejecting contaminated EEG epochs. It has been shown that ICA can effectively detect, separate and remove activity in EEG records from a wide variety of artifactual sources (Jung et al. 1998). The EEG signal was segmented into two sequences of 30 movements for the visual and the auditory condition, followed by segmentation into segments of 2-s duration. Each single subject provided 480 segments of 2 s, 240 from the auditory task and 240 from the visual task. Each movement is repre-

sented by eight segments of 2 s. Individual EEG data were additionally checked for muscle artefacts by visual inspection. Any segment still contaminated with artefacts was excluded from subsequent analysis. The 2-s segments were imported into LORETA software (<http://www.unizh.ch/keyinst/NewLORETA/LORETA01.htm>) in order to localise the intracerebral sources. Source estimation in LORETA is based on the assumption that the smoothest of all possible activity distributions is the most plausible to explain the data (Mulert et al. 2004; Pascual-Marqui et al. 1994; Pascual-Marqui et al. 2002). The single movements were then pooled to learning phases. Phase 1 includes the first ten movements, phase 2 the movements 11–20, and phase 3 the movements 21–30. Cross-spectra for the three phases were calculated for each subject.

In various studies changes in coherent brain activity are mostly seen in the alpha and the beta frequency range. Both frequency ranges have proved to be valuable in motor tasks (Andres et al. 1999; Classen et al. 1998; Gerloff et al. 1998; Manganotti et al. 1998). According to Pineda (2005) the alpha-like mu rhythm, typically identified as an 8–13 Hz oscillation, reflects several processes involved in the translation of visual and auditory representations into action-based representations. This function requires a global activation in the alpha frequency band realised through multiple alpha-domains, such as the visual-, auditory-, and somatosensory-centered domain.

Frequency bands are also often functionally divided into subbands (Klimesch 1999; Pfurtscheller et al. 2000; Pineda 2005). Klimesch distinguishes three alpha subbands that show different components. The lower two components are assumed to reflect general task demands and attentional processes, whereas the upper alpha band is associated with semantic processes. Because of large interindividual variance in alpha peak frequency, which, according to Klimesch, can be related to factors such as age, task demands and memory performance, individual definitions of frequency bands are proposed. Classically, the definition of individual alpha frequencies is based on alpha peak detection and usually determined by finding the maximum power within a certain frequency range in an eyes-closed EEG recording condition. However, most studies using individual alpha frequencies were carried out in the context of cognitive tasks. As we are investigating motor behaviour, the individual alpha peak was determined by pooling EEG data over the motor electrodes C3, CP3, FC3, FC4, C4 and CP4 and determining the strongest power value in the alpha-frequency range. Experiments from the Klimesch laboratory (1999) have shown that the transition to the theta frequency lies at about 4 Hz below the alpha peak. As the upper alpha band is supposed to be predominantly involved in semantic processing, we focused on the two lower alpha bands that reflect the general task demands.

This focus is supported by a motor study by Pfurtscheller et al. (2000) which shows that the lower alpha band is somatotopically non-specific and can therefore be discussed as mechanism that serves for general motor attention, whereas the upper alpha-band is somatotopically specific. The reason for concentrating on the lower alpha band is based on two aspects: First, because the individual alpha frequency is a prominent feature in the EEG oscillations it allows a relatively precise identification and quantification. Second, most importantly for this experiment is that the lower alpha band reflects general task demands and attentional processes. We anticipated that these psychological processes (general task demands and attention) will be involved in visuomotor learning as studied here (Praeg et al. 2005; Praeg et al. 2006; Toni et al. 2001). In addition, recent combined EEG and fMRI studies have elegantly shown that the alpha band negatively correlates with the BOLD response in parietal and frontal brain regions that are known to be involved in visuomotor control processes (Laufs et al. 2006a; Laufs et al. 2006b). The alpha band for each subject is defined as follows: 4 Hz bandwidth starting at the individual alpha peak towards lower frequencies. One subject had to be excluded as no peak between 5 and 14 Hz was discernable.

As mentioned above it is well established that parietal regions play an important role in conjunction with frontal structures in transforming visual to motor information. Areas in more inferior parts of the parietal lobe are important for audio-motor integration (Hickok and Poeppel 2000). We therefore defined three anatomical Regions of Interest (ROI) on each hemisphere: The first region covers the sensorimotor area, the second the superior and the third the inferior parietal region. The motor ROI was defined using MRICro (www.mricro.com) and is based on anatomical landmarks, as defined in earlier studies (Fink et al. 1997; Roland and Zilles 1996). Since LORETA data are present in the MNI space we used the MNI canonical template coming with the SPM package (SPM2, <http://www.fil.ion.ucl.ac.uk/spm>) to determine appropriate anatomical landmarks. The superior and inferior parietal regions were defined using a list of Brodman area information for LORETA voxels provided by the LORETA-KEY software package (<http://www.unizh.ch/keyinst/NewLORETA/LORETA01.htm>). The superior parietal ROI included the voxels corresponding to Brodmann area (BA) 7, the inferior parietal ROI included the voxels corresponding to BA 39 and BA 40.

In order to study the dynamic changes of functional coupling between these ROIs in relation to learning, coherence and phase locking were calculated for learning phases 1 and 3. Coherence and phase locking were calculated according to Eq. 1 for coherence and Eq. 2 for phase locking implemented in the LORETA software.

$$\text{Coh}_{\omega ij}^2 = \frac{[S_{r\omega}]_{ij}[S_{r\omega}]_{ij}^*}{[S_{r\omega}]_{ii}[S_{r\omega}]_{jj}} \quad (1)$$

where $S_{r\omega}$ is the cross-spectral matrix for the current density ROIs.

$$\text{PhL}_{\omega ij} = \left| \frac{1}{N} \sum_{k=1}^N \frac{[J_{r\omega k}]_i [J_{r\omega k}]_j^*}{\sqrt{[J_{r\omega k}]_i [J_{r\omega k}]_i^*} \sqrt{[J_{r\omega k}]_j [J_{r\omega k}]_j^*}} \right| \quad (2)$$

Phase locking computation is based on the collection of single epoch data (cross-spectral matrices of current density J) and the corresponding Fourier Transform for the ROIs.

Since Learners of the auditory and Learners of the visual condition are not necessarily the same subjects the two conditions are separately treated as follows: The coherence and phase locking measures were subjected to repeated measures ANOVAs with the two following factors: “phase” with two levels (1 = early, 3 = late) and “connectivity” with nine levels (inter-hemispheric: motor-motor, BA7-BA7, BA39/40-BA39/40; intra-hemispheric: motor-BA7, motor-BA39/40, BA7-BA39/40 of the left and the right hemisphere). Greenhouse-Geisser correction was used to guard against effects of heteroscedasticity. In case of significant main effects or interactions, post hoc *t*-tests were applied. To further test the relation between coupling and performance repeated measures regression analysis was employed (Lorch Jr and Myers 1990). In a first step regression analysis between phase locking (measured for each particular movement) and the averaged phase locking value for the respective subject was conducted to filter out the subject’s variance. In a second step, the residuals were correlated with performance (mean absolute deviation from target track) to test whether there is a significant correlation over subjects.

Results

Behaviour

Nineteen subjects performed the 30 movements of the visual task. In the auditory task, two subjects did not accomplish the task because their detection of the difference between the tones was too poor to fulfil correct task performance. Thus, only 17 subjects performed the 30 movements in the auditory condition. As mentioned above, one subject had to be excluded from further analysis because no alpha peak was detectable. In the visual condition, eight of the remaining 18 subjects were classified as Learners, and in the auditory condition, eight of the

remaining 16 subjects showed learning effects and were therefore classified as Learners.

The analysis of tracking performance (mean absolute deviation of steering-wheel movement from target track) over all subjects revealed a significant difference between the visual and the auditory task condition [ANOVA factor “condition”: $P < 0.001$, $F(1,12) = 27.8$, $\eta^2 = 0.70$]. In the visual condition, tracking performance was clearly better for all 30 movements. Tracking performance was even better right at the beginning of the visual task. In addition, tracking performance improved earlier for the visual than for the auditory task. In contrast to this, tracking performance improvement in the auditory task occurred more slowly and in smaller increments (see Figs. 3, 4). Furthermore, a significant main effect for the factor “phase” [$F(1,12) = 29.9$, $P < 0.05$, $\eta^2 = 0.72$] and a significant interaction “condition \times phase \times Learners” [auditory condition: $F(1,12) = 11.7$, $P < 0.001$, $\eta^2 = 0.49$; visual condition: $F(1,12) = 7.3$, $P < 0.05$, $\eta^2 = 0.38$] was registered. By visually comparing the performance of the Learners and the Non-Learners group a different pattern is obvious for the two modalities. In the auditory task subjects of the Learners group and the Non-Learners group start approximately on the same performance level. While the learners group show learning effects the subjects classified as Non-Learners remain on the base level. In the visual task however, subjects classified as Non-Learners started at a better performance level compared to the Learners group.

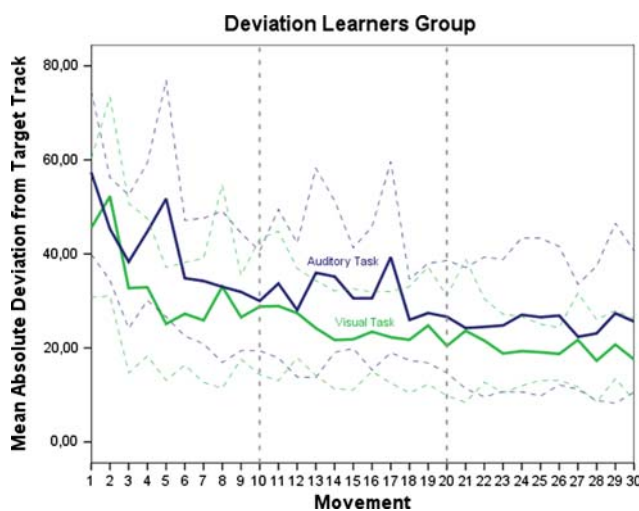


Fig. 3 Learning curve Learners group the figure shows the mean absolute deviation from target track (in degrees) computed for subjects of the Learners group of each modality. The learning curve from the visual condition is marked in green, the curve from the auditory condition in blue. Dashed lines of the respective colour indicate the learning curve \pm standard deviation. Subjects performed 30 movements, which were subsequently divided into three learning stages marked by the vertical line. Phase 1 contains movements 1–10, phase 2 movements 11–20 and phase 3 movements 21–30

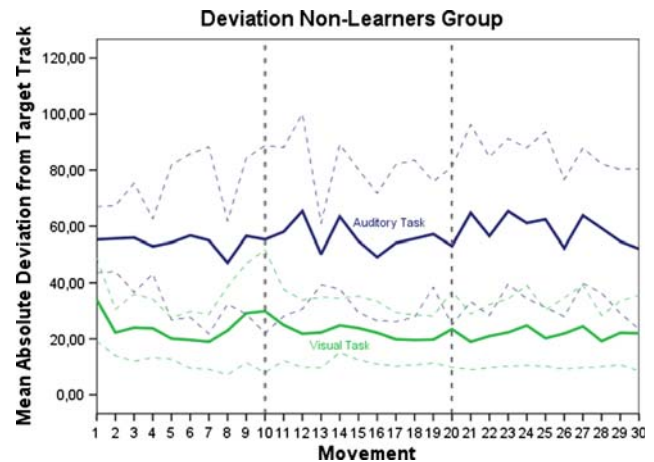


Fig. 4 Learning curve Non-Learners group. The figure shows the mean absolute deviation from target track (in degrees) computed for subjects of the Non-Learners group of each modality. The learning curve from the visual condition is marked in green, the curve from the auditory condition in blue. Dashed lines of the respective colour indicate the learning curve \pm standard deviation. Subjects performed 30 movements, which were subsequently divided into three learning stages marked by the vertical line. Phase 1 contains movements 1–10, phase 2 movements 11–20 and phase 3 movements 21–30

Although they had no prior experience of the task, no learning-related effects were registered because they showed skilled performance right at the beginning of the task. Since we were predominately interested in learning-related changes and not in differences in skill these group differences were not further investigated.

Coherences and phase locking

Given our main interest in learning-related changes we will focus on the subjects who were classified as Learners. Results from the Non-Learners group are not reported further. In the *auditory task* condition phase locking values differed significantly between phase 1 and phase 3 [ANOVA factor “phase”: $P < 0.05$, $F(1,7) = 5.9$, $\eta^2 = 0.46$]. Subsequent *t*-tests revealed that interhemispheric coherence increased significantly between the two inferior parietal ROIs ($P < 0.05$, $T = -3.03$, $df = 7$). The analysis for intra-hemispheric effects revealed significant increases between the motor ROI and the superior parietal ROI (BA7) in the left hemisphere ($P < 0.05$, $T = -2.41$, $df = 7$) (Table 1, Fig. 5). No significant main effects were evident for the coherence measures, and repeated measures ANOVA showed no significant main effects for the *visual task* condition.

Correlation coherence/phase locking and performance

Correlation analysis was restricted to performance and phase locking because learning-related changes were only

Table 1 Mean phase locking measures for the two learning phases (P1 and P3), the difference between both (P1 versus P3), and the effect size (Cohen's *d*). Standard deviations are given in brackets. Auditory task condition

AUDI/PL	P1	P3	P1 versus P3	Cohen's <i>d</i>
Mo-Mo	0.910 (0.019)	0.919 (0.015)	−0.009 (0.019)	−0.546
BA7-BA7	0.850 (0.046)	0.847 (0.064)	0.003 (0.033)	0.049
BA7-BA39/40 r	0.367 (0.092)	0.397 (0.087)	−0.029 (0.048)	−0.330
BA7-BA39/40 l	0.350 (0.060)	0.349 (0.085)	0.001 (0.058)	0.010
Mo-BA7 r	0.328 (0.047)	0.357 (0.063)	−0.029 (0.038)	−0.523
Mo-BA7 l	0.325 (0.055)	0.354 (0.059)	−0.028 (0.033)	−0.500
BA39/40	0.255 (0.066)	0.297 (0.072)	−0.042 (0.040)	−0.615
Mo-BA39/40 l	0.237 (0.027)	0.249 (0.062)	−0.011 (0.043)	−0.238
Mo-BA39/40 r	0.205 (0.066)	0.197 (0.070)	0.008 (0.028)	0.114

AUDI auditory task condition, PL phase locking, P1 phase 1, P3 phase 3, P3 versus P1 comparison phase 3 versus phase 1, Cohen's *d* the difference between two mean values divided by the accompanying standard deviation (0.2 indicative of a small effect, 0.5 a medium and 0.8 a large effect size), connectivities—inter-hemispheric: Mo-Mo motor areas, BA7-BA7 superior parietal areas, BA39/40 inferior parietal areas, intra-hemispheric: Mo-BA7 l motor–superior parietal area, left hemisphere, Mo-BA7 r motor–superior parietal area, right hemisphere, Mo-BA39/40 l motor–inferior parietal area, left hemisphere, Mo-BA39/40 r motor–inferior parietal area, right hemisphere, BA7-BA39/40 l superior parietal–inferior parietal area, left hemisphere, BA7-BA39/40 r superior parietal–inferior parietal area, right hemisphere

Significant ($P < 0.05$) values are given in italics

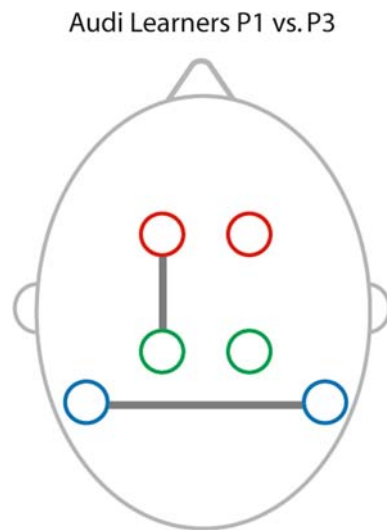


Fig. 5 Learning-related changes of coupling *solid lines* show significant changes of the phase locking measures from phase1 (P1) to phase 3 (P3). Audi Learners: auditory task condition, Learners group. Motor ROIs in *red*, superior parietal lobule ROIs in *green*, inferior parietal lobule ROIs in *blue*

detectable in the phase locking measure. In the *auditory task* condition the Learners showed no significant correlations between performance and phase locking. In the *visual task* condition better tracking performance of the Learners group was positively correlated with higher intra-hemispheric phase locking between the motor and superior parietal regions bilaterally [left hemisphere: $r^2 = -0.150$, $F(1,209) = 4.97$, $P < 0.05$; right hemisphere: $r^2 = -0.153$, $F(1,209) = 5.20$, $P < 0.05$] (Table 2, Fig. 6). Because this test is somewhat anticonservative, we also

calculated *p* values according to the most conservative estimation of degrees of freedom ($df = 1,7$) with which we obtained a $P = 0.06$ for $F = 4.97$ and a $P = 0.05$ for $F = 5.20$.

Discussion

The present study was designed to examine cortical coherence and phase locking between brain areas known to be involved in sensorimotor control during the course of motor learning. The learning task was based on a visually and auditorily guided tracking movement. We expected that performance would rely on cooperation between sensory and motor areas, and that appropriate transformations of sensory signals into codes appropriate for movement control are therefore needed. Thus, the first aim of this study was to trace learning-related changes of coupling in the motor and parietal areas. For example, we were interested to know between which areas changes in coherence and phase locking occur over the time course of learning. The second aim was to determine if there is a correlation between coherence and movement performance. In addition, we were interested in studying possible differences between auditorily and visually guided tracking movements both in terms of movement precision and cortical coherence. Visual and auditory tracking differed considerably in terms of movement precision, the visual task being altogether the easier of the two. For this reason, the coherence and phase locking findings will be discussed separately, first for the auditory and then for the visual motor learning task.

Table 2 Correlation of “phase locking” with “mean absolute deviation” from target-track. Visual task condition

VIS/PL	Correlation
Mo-Mo	-0.121
BA7-BA7	-0.104
BA7-BA39/40 r	0.023
BA7-BA39/40 l	0.018
Mo-BA7 r	-0.153
Mo-BA7 l	-0.150
BA39.40	0.020
Mo-BA39/40 l	0.042
Mo-BA39/40 r	0.132

VIS visual task condition, correlation: one-tailed Pearson's *r*-values. connectivities—inter-hemispheric: *Mo-Mo* motor areas, *BA7-BA7* superior parietal areas, *BA39/40* inferior parietal areas, intra-hemispheric: *Mo-BA7 l* motor–superior parietal area, left hemisphere, *Mo-BA7 r* motor–superior parietal area, right hemisphere, *Mo-BA39/40 l* motor–inferior parietal area, left hemisphere, *Mo-BA39/40 r* motor–inferior parietal area, right hemisphere, *BA7-BA39/40 l* superior parietal–inferior parietal area, left hemisphere, *BA7-BA39/40 r* superior parietal–inferior parietal area, right hemisphere

Significant ($P < 0.05$) values are given in italics

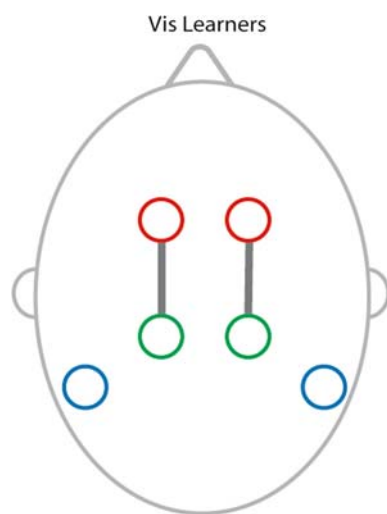


Fig. 6 Correlation of coupling with performance *solid lines* show ROIs between which “phase locking” positively correlated with “mean absolute deviation from target-track”. VisLearners: visual task condition, Learners group. Motor ROIs in *red*, superior parietal lobule ROIs in *green*, inferior parietal lobule ROIs in *blue*

Compensatory tracking learning under auditory guidance

The more demanding auditory condition revealed enhanced inter-hemispheric phase locking in the alpha band between the inferior parietal regions. The coupling of these regions should be interpreted in the light of recent findings from auditory perception research. As shown by several authors

(Baumann et al. 2006; Gaab et al. 2003; Hickok and Poeppel 2000; Warren et al. 2005), brain areas in the vicinity of the supramarginal and angular gyrus extending into the posterior part of the planum temporale (predominantly in the left hemisphere) are involved in audiomotor integration processes. Accordingly, we hypothesise that increased coherence between the inferior parietal areas during auditory guided tracking movement reflect the coherent involvement of these areas in audiomotor integration.

Inspection of the intra-hemispheric coupling revealed a significant increase between the motor and the superior parietal region in the left hemisphere. In the context of the findings of Classen et al. (1998) that coherent brain activity reflects integrative sensorimotor behaviour, our results indicate integration processes of spatial information, attributed to parietal regions, and movement execution, linked to motor areas. Thus, synchrony between the superior parietal region and the motor area in the hemisphere contralateral to the dominant hand might be important for task-related successful movement execution. The predominant role of the left hemisphere during control of bimanual movement is supported by functional imaging work that has demonstrated substantial left hemisphere involvement during bimanual assignments in right-handed persons (Jancke et al. 1998). Further evidence for the importance of the dominant hemisphere in right-handed subjects is provided by studies of Serrien et al. (2003) and Pollok et al. (2005).

In contrast to the studies of Andres et al. (1999) and Gerloff and Andres (2002), who report increased coherence between motor areas during learning of bimanual movements, no such inter-hemispheric changes in coherence were registered in the present study. However, Gerloff and Andres reported that an increase in functional inter-hemispheric coupling between motor areas is only evident during early stages of bimanual co-ordination learning and not during learning of unimanual sequences, or during repetition of sequences. Overlearned bimanual movements, on the other hand, revealed a subsequent decrease in inter-hemispheric coupling. Relating our findings to previous motor studies that used coherence measures is however complicated because different movement tasks were adopted. For example, Serrien and Brown (2003) used a bimanual coordination task without external sensory guidance and found decreased coherence between the motor areas in the alpha and beta bands with increasing practice (during early learning stages); with increasing bimanual proficiency both motor areas are obviously operating in an uncoupled manner. There was also an increased interhemispheric coherence in the gamma band between prefrontal regions. In conclusion, the cortico-cortical connectivity might vary across regions and EEG band frequencies in dependence on the task used. Unlike the tasks used in these studies, our task requires bimanual

control of a steering-wheel, and therefore involves a kind of in-phase bimanual movement which is continuously controlled by auditory or visual feedback. We hypothesise that in our study external guidance is optimised during learning, while in the studies of Serrien and Gerloff an internal control mode is implemented with increasing practice.

Learning-related effects were only reflected in the phase locking measure. In the coherence measure similar effects as in the phase locking measure did occur but no significant learning-related changes were detectable. This is consistent with the finding of Lehmann et al. (2006), who reports that phase locking values are not very different from coherence values. Coherence is a measure that does not differentiate between the effects of amplitude and phase in the relation between two signals. In contrast, phase locking is determined only by the phase component of two oscillating signals. The present results suggest that changes, which accompany a learning process, are generated by effects of synchrony rather than effects of amplitude. Although a difference in coherence and phase locking is reported here, a clear distinction between different patterns is not discernable on the basis of the present study. Revealing the contribution of amplitude and synchrony to communication between brain areas may represent a challenge for which studies would need to be especially designed.

While learning-related changes were registered by comparing phase 1 versus phase 3, performance did not significantly correlate with the phase locking measures. We assume that the demanding performance in the auditory task condition is influenced by other factors such as attentional processes and is therefore not solely dependent on coupling of important areas like the inferior parietal regions. Subjects seem less accustomed to performing auditorily guided tracking movements, and this may result in a greater impact of various error sources on performance. This suggestion may find support in the behavioural data. In contrast to the visual condition, in which the ‘‘Learners’’ showed a mean absolute deviation from target track of $33.1^\circ \pm 10.7^\circ$ in phase 1 and a mean absolute deviation of $19.9^\circ \pm 7.6^\circ$ in phase 3, the mean absolute deviation of the ‘‘Learners’’ in the auditory task condition was much higher (phase 1: $40.2^\circ \pm 12.4^\circ$, phase 3: $25.3^\circ \pm 14.0^\circ$).

Compensatory tracking learning under visual guidance

Although the performance of the Learners group was significantly better in phase 3 compared with phase 1, no significant differences in coherence measures were registered. Learning effects are therefore not reflected in changes of coherent neuronal activity in the individual alpha band. First and as mentioned above, the mean absolute

deviation was generally smaller in the visual condition than in the auditory condition. This indicates that the visual task was easier to perform; this was the view expressed informally by most subjects. Second, a decrease of the mean absolute deviation from the target track is already seen over the first ten movements, which may indicate that subjects built the pattern of coherent brain activity during this early learning phase. In the visual condition, learning effects from phase 1 to phase 3 may therefore be too small to be reflected in changes of coherence of cortical oscillations. Assuming that changes in coherence of oscillations in the alpha range are indicative of changes in general task demands, the task demands in phase 1 are comparable to those in phase 3. While not evident in the auditory condition, significant correlation of performance with phase locking was observed in the visual task condition: better tracking performance correlated positively with higher intra-hemispheric phase locking values between the motor and superior parietal regions bilaterally. We therefore assume that the relative influence of other factors than sensorimotor integration processes was smaller in the easier visual task condition compared to that in the auditory task condition, and that this is also reflected in smaller variance of the single trials in the visual condition. Thus, phase locking between sensorimotor regions may be regarded as proximate determinants of performance. The involvement of parietal regions is well known in spatial transformation processes and visual spatial attention (Chambers et al. 2004). Learning of movements requiring transformation processes has been shown to involve a fronto-parietal network (Floyer-Lea and Matthews 2004; Frutiger et al. 2000), which supports the role of intra-hemispheric coupling of motor and parietal regions as a basis for good performance.

Conclusion

The present study provides an interesting insight into the organisation and re-organisation of brain areas during early sensorimotor learning and reveals mechanisms recruited by the brain to successfully cope with task requirements. First, the general task demands differed between the auditory and the visual condition. The visual task seemed easier to perform than the auditory task, which might be related to the general predominance of the visual modality in everyday life. Second, the following conclusions may be drawn about *auditory guidance*: The coherence analysis indicates the importance of inter-hemispheric coupling between the inferior parietal regions. This collaboration is probably of chief importance in subserving the guidance of movement by external auditory stimuli, and may be essential to successful performance of the auditory task. In

addition, the learning-related increase in intra-hemispheric coupling between motor and superior parietal area in the left hemisphere is indicative of integrative processes of spatial information and movement execution. Third, the correlation analysis for *visually guided movements* corroborates the relevance of intra-hemispheric coupling of motor and superior parietal regions. These results and those of the coherence analysis of the auditory task show that this motor-parietal network is activated in both the auditory condition and the visual condition. Finally, the present study confirmed that frontal and parietal regions are strongly involved in continuous tracking movements which require sensorimotor transformation processes. The results suggest that continuous tracking movements are continuously controlled by auditory or visual feedback throughout the learning stages. It may therefore be speculated that increasing practice is not accompanied by a decrease in coherence between the areas involved. This suggestion has to be clarified in a further study of overlearned tracking movements.

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